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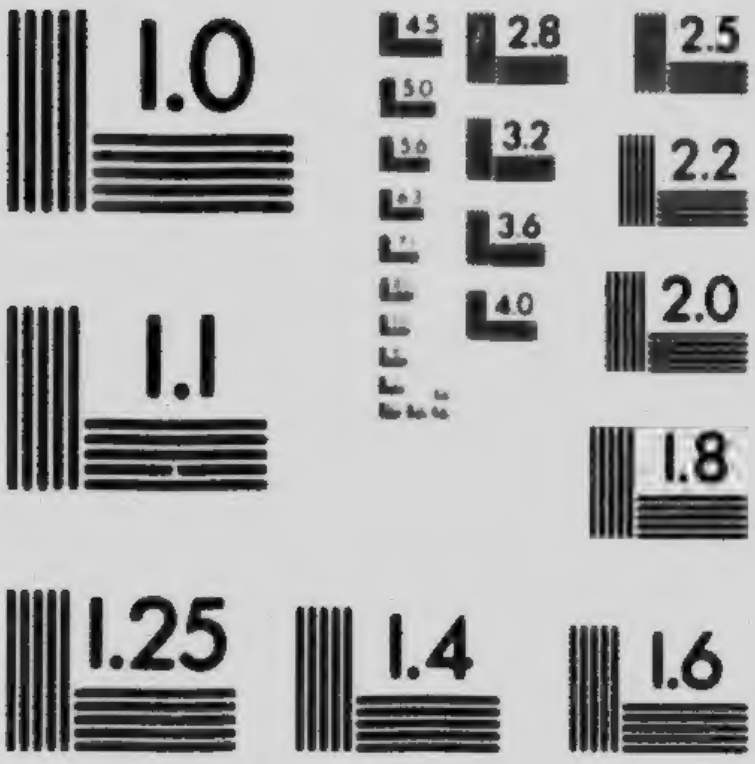

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No. 6: ON POLYSTELY IN ROOTS OF ORCHIDACEAE, BY J. H. WHITE

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ON POLYSTELY IN ROOTS OF ORCHIDACEAE

BY

J. H. WHITE, B.A.

BIOLOGICAL SERIES No. 6

ERRATA

Page 7 [169] line 23 should read:
"Split off from the large stele, itself underwent division. The"

Page 10 [172] line 9, for "monostele" read "stele."

Page 11 [173] line 2, after "root" insert "in *H. hyperborea*."

Page 12 [174] line 14, after "*H. orbiculata*" insert "and *H. blephariglottis*"

Page 14 [176] line 10, after "*H. orbiculata*" insert "and *H. blephariglottis*"

Page 15 [177] line 3-4, omit the word "extra-stelar," and line 21, after "placed" insert "by these botanists."

Page 18 [180], third reference from the bottom (Strasburger, Lehrbuch der Botanik) for '03 read '04.

Plates I & II, heading, for "Biological Series No. 7" read "Biological Series No. 6."

PREFATORY NOTE.

The work embodied in this article was done by Mr. J. H. White, while pursuing graduate studies in Botany in the University of Toronto, during the year 1906-07.

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Lecturer in Botany.

ON POLYSTELY IN ROOTS OF ORCHIDACEAE.

In his essay on polystely Van Tieghem ('80) defined polystely as follows: "Les faisceaux conducteurs peuvent être groupés en plusieurs cercles autour d'autant d'axes diversement disposés, de manière à constituer tout autant de cylindres centraux distincts, ayant chacun sa moelle, ses rayons médullaires, son pericycle et son endoderme, tous reliés et enveloppés par une écorce commune. . . . La disposition de l'appareil conducteur est polystélique." This condition he conceived to be derived by repeated division of the monostele. He based this view on his conception of the anatomy of the stems of *Primula*, *Gunnera*, etc., and extended his conclusions to the stems of most vascular cryptogams. As regards polystely in roots, he described but one example—some of the roots in certain Lycopodineæ.

Van Tieghem mentioned the "tubercules" of *Orchis*, *Ophrys*, etc., which show numerous steles, only to state that they merely simulate polystely. "Les tubercules des *Orchis*, *Ophrys*, etc., possèdent, comme on sait, un plus ou moins grand nombre de stêles distinctes dans une écorce commune, mais toutes ces stêles s'attachent independamment, quoique en des points très voisins, sur le rameau qui porte le tubercule; elles ne dérivent pas l'une de l'autre par voie de division. Ce tubercule est donc constitué par un faisceau de racines concrescentes et non par une racine polystélique. C'est un des exemples qui montrent le mieux combien il est nécessaire de dégager la polystélique vraie des illusions produites par la concrescence."

Polystely in stems has received the attention of several investigators since Van Tieghem's time, with the result that it has been disproved. Leclerc du Sablon ('90) has shown that the numerous strands in the stem of *Pteris* do not originate by division of a monostele. Likewise, Gwynne-Vaughan ('97) has disproved Van Tieghem's statement in regard to *Primula*. Jeffrey ('00, '02), by an exhaustive study, has shown that in none of the so-called polystelic Pteridophyta, nor in the few

cases among the Angiosperms, is this condition due to bifurcation of a single stele. Instead, it has been proved that the central cylinder is always a monostele, and that the gaps caused by the departure of the foliar and ramular traces from a medullated monostele furnish the explanation of the so-called polystelic type.

Polystely in roots has likewise received some attention, and it is said to exist in the tuberous or abnormal roots of the Leguminosæ, Cycadaceæ, and Palmaceæ. Of these, the roots of the Palmaceæ have been most carefully examined, notably by Cormack ('96) and Drabble (:04). Cormack discovered what he considered to be polystely in this group, and his observations have been corroborated by Drabble, and summarized as follows: "Cormack grouped the arrangements met with under several headings, commencing with the normal type possessing a complete endodermis surrounding a central fibrous or sclerenchymatous ring in which lie the xylem and phloem elements. Passing through the condition in which the cylinder is still complete, but longitudinally lobed, the endodermis dipping into the depressions, but being quite continuous, he came to those roots in which the central cylinder is composed of a series of independently running strands of fibrous tissue presenting the form of arcs of circles in transverse section; between these the endodermis dips in and becomes discontinuous; and, finally, he described the case of *Areca*, where one or more of these independent strands presents a complete radially symmetrical cylinder or 'stele,' as he terms it, round which the endodermis is complete." Drabble points out that the "polystelic" condition is restricted to the proximal portion of the roots; the distal is always that of a normal monostelic root. Whatever interpretation may be placed upon these observations, it will be seen that the phenomena to be described in the roots of the Orchidaceæ differ in some respects from those in the Palmaceæ.

Since Van Tieghem's time no comparative investigations of the multistelic roots of the Orchidaceæ have been made to determine the homologies of their stelar system, and all later references agree with his views.

Strasburger (:04), in his text-book of botany, says: "Einen eigenen morphologischen Aufbau zeigen die Knollen der Orchideen. Sie werden der Hauptmasse nach aus fleischig

angeschwollenen, nicht von einander gesonderten Wurzeln gebildet, oben schliessen sie aber mit einer Stammknospen ab" (p. 40, also p. 435). Schumann (1902) says: "Wenn man den Namen Polystelie dennoch beibehalten will, so kann man diesen anwenden auf diejenigen Fälle wie die Orchideenwurzelknollen, wo durch Verwachsen mehrerer Wurzeln ein einheitlicher Körper entsteht, der wirklich mehrere Stelen führt. Bekanntlich bezeichnet aber gerade Van Tieghem diesen Fall nicht als Polystelie, weil er hier durch Verwachsen entstanden ist" (p. 156).

These views, however, have not seemed conclusive, and the present investigation was begun with a view to determine, first, the structure of the roots of terrestrial Orchidaceæ, and secondly, the interpretation of their structure in terms of modern stelar hypotheses.

The roots of these Orchids are outgrowths of an adventitious shoot—a fact due to the habit of vegetative reproduction characteristic of these plants. Each year one or more stolons are developed, each of which produces a new bud. The old plant dies away, and the adventitious shoot perpetuates the species the following season. In connection with this method of reproduction many of these Orchidaceæ show a differentiation of the root system into a primary tuberous root—part of the so-called "tuber" and having the characters of a storage root—and somewhat slender lateral roots. This is especially true of the Ophrydinæ. It is in the roots of this class of Orchidaceæ that there is an appearance of polystely, and it is with the anatomy of these alone that we are here concerned.

THE LATERAL ROOTS

Among the lateral roots there are two types, the monostelic and the polystelic. The monostelic type is characteristic of *Habenaria bracteata*, R. Br., *H. repens*, Nutt, *Orchis spectabilis*, L., and some of the roots of *H. orbiculata*, Torr. In these forms there is a single stele, consisting of bast and wood elements arranged fairly radially around a central pith, and surrounded by an endodermis. As a rule the bast is not very well developed. The strands composing this stele come from different parts of the vascular supply of the stem,

just as in the case of such monostelic genera as *Goodyera*, *Epipactis*, etc. Plate I, figure 4, represents a transverse section of the stele of *H. bracteata*. In the apical region there is a well-formed root-cap, and just back of it the meristem from which are differentiated the three embryonic regions, namely dermatogen, periblem and pierome.

The polystelic (pseudo-polystelic, according to Van Tieghem) type is not mentioned by Van Tieghem as occurring in the lateral roots, but has been described by Holm (:04) in several forms. *Habenaria orbiculata* furnishes examples of distelic roots, and there are indications of distely in *Orchis spectabilis*. In the latter species many cases were met with in which the stele showed a distinct flattening, and while no case of two steles was seen, it is very probable that this condition sometimes occurs. The lateral roots of *H. orbiculata* are always monostelic at their base. Farther out, the stele in some of them flattens, and still farther out, assumes a horse-shoe shape. Plate I, figure 6, represents the stele of *H. orbiculata* when just beginning to flatten, and Plate I, figure 7, the latter condition. Farther out still, the stele is constricted into two equal parts (Plate I, figure 8), or in other words, by an act of bifurcation, the monostele gives rise to two steles, a phenomenon that Van Tieghem apparently could not have observed, standing as it does in direct opposition to his statement on the subject (Van Tieghem and Douliot ('86). These strands continue side by side throughout the greater part of the root. At the tip of the root a typical root-cap is present, and just behind it a single meristem giving rise to a single dermatogen, periblem, and plerome. At some distance back the primary plerome strand gives rise to two secondary plerome strands corresponding to the two steles and to the ground tissue separating them. Each of these steles is a typical root stele, possessing alternate bast and wood elements, and each is enclosed by an endodermis. As already stated, the roots of *H. orbiculata* are not always distelic, those of the earlier generations and the smaller ones being monostelic throughout.

Of the polystelic type none is of greater interest than the roots of *H. blephariglottis*, Hook. In these the strands composing the root stele bear the same relation to the vascular supply of the stem as in the case of any monostelic form, such as

H. bracteata. Each of the lateral roots in most of the specimens that were examined was found to be monostelic at its base as in *H. orbiculata.* It is in many cases protostelic for some distance out, and then becomes siphonostelic, owing to the appearance of a pith and an internal endodermis (Plate I, figure 1), a condition that is unique in the structure of root steles. Farther out from the stem a gap appears in the stele, through which the pith and cortex connect, and the internal and external endodermes become continuous (Plate I, figure 2, *a*). As the series is followed on in the same direction the gap enlarges, giving the stele a horse-shoe shape. Successive acts of segmentation then take place, steles being pinched off from the ends of the shoe, more or less alternately (Plate I, figure 3), till finally in place of the monostele there is a number of small steles of approximately the same size regularly arranged in a circle. Each of these small steles has the bast and wood elements arranged in an irregularly radial manner (Plate II, figure 10).

The roots of this species that were examined showed only minor points of difference among themselves, such as a smaller or a larger number of steles, according to the size of the root, or an at first scattered, irregular, instead of circular arrangement of the individual steles. In some cases a stele, after being roots of *H. hyperborea,* R. Br. (Plate II, figure 9). The main fact held for most of them, namely, that the individual steles were derived by a process of segmentation from a monostele. Occasionally, however, in robust roots, the conditions at the base approach those in *H. hyperborea.*

In more specialized forms the fibro-vascular supply comes off from the stem in a small number of steles, as, for example, in the roots of *H. hyperborea,* R. Br. (Plate II, figure 9). The origin of the strands composing these steles is in no way different, however, from what obtains in the three species already described. The small number of steles seems to mean that the division of the monostele is carried back to the stem connection. Farther out these steles are to be found undergoing division, resulting in a large number of small steles of approximately the same size, just as in *H. blephariglottis* (Plate II, figure 10).

The tip in all these polystelic roots is clothed by a single root-cap, just as in *H. orbiculata,* behind which is a small-celled meristem from which all of the organs of the root originate.

It is worthy of note from a phylogenetic standpoint that in the roots of plants of younger generations the number of steles is very much smaller than in those of older generations. For example, in the roots of plants of *H. orbiculata* belonging to very early generations never more than one stele was present; in *H. hyperborea* as few as two were found, and in *H. blephariglottis* the number was likewise small. The increase in the number of steles in the roots of plants of each succeeding generation from the seed till the flowering plant is reached without a proportionate increase in the number of steles entering these roots, and without any indication of a disturbance of the conditions described in the *punctum vegetationis* of each, seems out of accord with the theory of concrescence.

Examination of very young plants in a number of species, where the roots were just beginning to grow out from the stem, showed that but one meristematic mass was present, and in no case was there any indication of a fusion of two or more roots. In accordance with the view that the phylogeny of the race is recapitulated in the ontogeny of the individual, one might have expected to find, in some cases at least, discrete meristematic areas corresponding to component roots, if the concrescence theory were correct; but one for each root is the invariable rule.

The other polystelic species examined were *H. clavellata*, R. Br., *H. psycodes*, Gray, *H. virescens*, Spreng, *H. lacera*, R. Br., *H. obtusata*, Rich., *H. leucophaea*, Gray, and *H. Hookeriana*, A. Gray. The structure of the roots of these species agrees very closely with that just described for *H. hyperborea*.

THE PRIMARY ROOT OF THE "TUBER"

As already stated, vegetative reproduction is characteristic of terrestrial Orchidaceæ, and in many of them the adventitious shoot is tuberous. A typical "tuber" consists of a stolon or rhizome bearing a lateral bud, from which in turn there is developed an axial tuberous root, occupying the position of a primary root. Among the "tubers" there is much variation in the length of the stolon, and the direction of the axis of the root. Thus in *H. bracteata* and *H. orbiculata*, for example, the stolon is very short, whereas in *H. clavellata*, *H. blephariglottis* and *Orchis spectabilis* it is comparatively long. In most of

these Orchids the primary root is vertical, but there are all gradations to the horizontal position assumed in the case of *H. dilatata*, Gray. There may be even some variation in the same species. Thus in *H. hyperborea* there is considerable variation in the length of the stolon, and it is noticeable that an increase in the length of the stolon is accompanied by a greater departure of the root from its usual vertical position.

The stolon possesses a single stele of cauline structure. There is a continuous ring of xylem around a central pith, with the bast externally placed, and the whole is surrounded by an endodermis, that is, there is an ectophloic siphonostele (Plate I, figure 5). This seems to agree with the primitive monocotyledonous type of cauline stele as defined by Chrysler (:04), and Plowman (:06). This siphonostele goes to supply the young shoot and its root.

Characteristically the primary axial root is polystelic, the number of steles varying from as few as two in *Orchis spectabilis* to twenty or more in *H. blephariglottis*. It remains now to be determined whether these are steles of a fundamentally unit root, as has been shown to be the case in the lateral roots, or monosteles of concrescent roots. Among the lateral roots, as has been seen, there are both monostelic and polystelic forms, with instances of distely occurring in *H. orbiculata* as a connecting link. All of the lateral roots, except the most specialized forms, are monostelic at their base, the root tips of all show but one small-celled meristem (Plate II, figure 1[illegible]nd the young roots originate each from a single meristematic area. A careful examination should reveal the extent to which these conditions prevail in the axial roots.

In the transitional region between stem and axial root, in a form such as *Orchis spectabilis*, the stolon siphonostele gives off the vascular axis of the adventitious bud, and a pair of steles which turn down into the tuberous root. Almost immediately in some plants a third root stele is given off. After supplying the bud the siphonostele at once becomes much attenuated, curves down, and ends in a minute projection of meristematic tissue on the surface, on the way giving off a single trace to a leaf which sheathes the new shoot. The meristematic projection is the tip of the stolon, and hence the adventitious bud is distinctly lateral. The three root steles do not form a mono-

stele at their base, though they leave the stolon at practically the same level. They recall the condition of affairs in the base of the lateral roots of *H. hyperborea* (Diagram 1). Much the same phenomena obtain in the case of *H. orbiculata* (Diagrams 2-13). Here a pair of root steles is given off just as in *Orchis*, but the third stele is given off at a lower plane. Usually this third stele soon bifurcates, so that of the four steles present in the axial root two, at least, are obviously derived from a pre-existing monostele by an act of bifurcation.

In those forms which have acquired a diageotropic habit, as, for example, *H. clavellata*, the origin of the root steles is very diffuse—a phenomenon on which Van Tieghem based his main argument in support of the concrescence theory. The stolon has the same mode of origin as in the preceding forms, and possesses a similar siphonostele. Serial sections show that this siphonostele soon begins to give off steles. These are very small and are usually given off right and left alternately, while the remainder of the siphonostele continues on in the same relative position. They slant downward and run along close to the ventral surface, the whole of them forming an arch when viewed in transverse section. These small steles are usually all derived from the main stele; only very rarely does one of them bifurcate after being given off. A marked difference is observable in the character of the cortex in the dorsal and ventral regions, in that the cells of the dorsal region are smaller and more compact than those of the ventral. From the dorsal portion of the siphonostele the stele to the new shoot is given off. As in the forms already described, the stele of the stolon then becomes abruptly attenuated, gives off one or two more root steles, curves up, and ends in the stolon tip on the dorsal surface, on its way giving off the leaf trace. It is important to note that in spite of their very diffuse origin all of the steles given off along the stolon proceed to the tip of the tuberous root, and end in one meristematic area in the growing point, just as in all the other species examined (Diagram 14).

On comparing this form with *Orchis* and *H. orbiculata* it is noteworthy that there is no difference other than that the root steles have a more diffuse origin—a phenomenon that is probably to be accounted for by the unusual position of the root. That this is the case is well shown by *H. hyperborea*. As

already stated there is much variation in the length of the stolon and the position of the root, the two being associated more or less. In those cases where the stolon is extremely short and the axial root accordingly perpendicular, no steles are given off throughout the length of the stolon proper, and the origin of the root steles is no more diffuse than in *Orchis* or *H. orbiculata*. But in those instances where the plant puts forth a long stolon and the axial root takes on a slanting position, steles are given off as in *H. clavellata* (Diagrams 15-26). Hence, it seems evident that the diffuse origin of the root steles in forms like *H. clavellata* is to be ascribed to the diageotropism of the root. It might be stated here that in *H. blepharíglottis*, where the position of the root comes nearest, of the species examined, to that of *H. clavellata*, the degree of diffuseness of the root steles is intermediate between the condition in *H. hyperborea* and that in *H. clavellata*.

Plants of *H. hyperborea* of a very early generation possess another feature, however, of even greater import. For several sections below the region of the stolon stele, that is, at the upper end of the axial root, all of the vascular elements are enclosed within one endodermis. This single root stele then simultaneously breaks up into the two or three steles which are present throughout the remainder of the axial root to its tip (Diagram 27), a fact that amounts almost to a demonstration that the axial root is a unit, and not the result of concrescence.

Thus there is a fairly complete series, in the case of the axial or tuberous root, from the monostelic to the most extreme polystelic type, which parallels closely what has been already described for the lateral roots.

It is further to be noted that the tip of the axial root has a single root-cap, and behind it the meristem, which is differentiated as in the lateral roots. Figures 11, 12, 13, of Plate II, are from serial sections of the tip of the axial tuberous root of a plant of *H. hyperborea* of an early generation, in which there is a primary plerome strand that is continuous proximally with secondary plerome strands. Occasionally the tip is forked, as, for example, in *H. bracteata*. This forking, however, occurs only in the older roots, and seems to be of the nature of a splitting or dichotomy, and bears no relation to the number of steles. Apparently the root tip is first flattened, and a meri-

stematic area in the centre of the tip ceases growing, while the isolated areas on either side continue their growth, which results in the forking just mentioned. Drabble (:04) has figured a similar forking in *Kentia*, Sp.

The same fact has been observed with regard to the tuberous roots as was seen in the lateral roots, namely, that in those of the earlier generations the number of steles is much smaller than in those of the later generations. Thus it is not uncommon in *H. bracteata* to find three steles in the axial root of one generation, and six steles in the corresponding root of the next generation. Again, in the tuberous root of *H. hyperborea* of a young generation (Diagram 27) two steles were found, while the next generation showed very many more, and in early generations of *H. orbiculata* there is but one. It is altogether probable that in the earliest generations of all of them there is but a single stele.

THE "TUBER"

Van Tieghem looked upon the "tuber" as a branch carrying a "tubercule" with a greater or smaller number of distinct roots, the steles of which attach themselves independently, though at points very close together, on the branch. According to him, the "tubercule" is a bundle of concrescent monostelic roots, and not a single polystelic root. Others have gone further and included more in the concrescence. Thus, Germain de St. Pierre ('55) includes in it stem and leaf portions as well as roots, and he has lately been followed by Holm (:04). But according to the foregoing observations on the primary root of the "tuber" taken in conjunction with those on the lateral roots, the "tubercule" is simply a swollen root which is usually polystelic. One other fact has been overlooked in previous accounts of the "tuber," namely, that the stolon continues beyond the origin of the adventitious shoot, and that the leaf ensheathing the upper part of the "tuber" derives its vascular supply from the distal portion of the stolon.

CONCLUSIONS

The "concrescence" theory has been stated already. The grounds on which this view is based are the diffuse origin of the steles of a tuberous root, and the forking of the root tips in

forms such as *H. bracteata* and *Orchis latifolia*. But in the light of the foregoing observations these grounds are scarcely tenable.

The forking of tuberous roots is apparently a matter of accident. There is no indication of it in young roots prior to the differentiation of the steles. Moreover, it bears no relation to the steles. Forking is not characteristic of the more slender roots, and it is never present in lateral roots, nor even in the markedly multistelic roots of *H. clavellata*, though not of infrequent occurrence in swollen roots of several other species. The forking is probably caused by purely mechanical forces, and in view of the facts recorded of the earlier stages of development can be regarded in no way as indicating concrescence.

It is apparent from former accounts that the theory of concrescence has been based on an examination of the tuberous roots only. To understand the structure of these, however, in regard to the origin of the steles, the conditions obtaining in the lateral roots are of material assistance. Thus it has been seen that the lateral roots of *H. bracteata* exhibit typical monostely, and the other species may be looked upon as presenting deviations from this type. Of these, *H. orbiculata* shows the least deviation, only some of the roots being distelic, and these for the central portion only of their length. The roots of *H. blephariglottis* are characterized by a still greater deviation, in that they possess more than two steles, but although this is the case they are characteristically monostelic at the base, and hence can only be looked upon as single roots. *H. hyperborea* departs from the type more widely still, in that the roots are never monostelic at the base. However, the fact that they possess but a few steles in this region, and that the larger number farther out is derived from these by segmentation, shows the tendency towards the condition in *H. blephariglottis*, and may be taken to indicate that the division of the monostele has been carried back into the stem. To cite an analogous case, the carrying back of the cleavage of a fibro-vascular strand to its origin is seen in the leaf traces of certain ferns. Primitively the foliar fibro-vascular supply in the *Filicales* comprises a single strand, but in many of the more specialized ferns this strand is divided, and commonly the segments are attached separately to the stelar axis of the stem. Indeed, the facts relative to the origin of the steles

in multistelic lateral roots point to the conclusion that they are the result of the segmentation of a single stele, and are not indicative of concrescence of several monostelic roots.

The steles of the multistelic axial or tuberous roots are much more frequently attached separately to the cauline stele than is the case in the lateral roots, but this phenomenon is not as universal as Van Tieghem thought. In fact, segmentation of a root stele is by no means infrequent, and sometimes monosteles exist at the base of axial roots in earlier generations. Thus, the tuberous roots of early generations of *H. orbiculata* are monostelic throughout, and what may be considered of greater significance, corresponding monosteles in *H. hyperborea* divide after leaving the stem, plainly fulfilling the conditions expressed by Van Tieghem in his definition of polystely. Moreover, the most striking examples of a diffuse origin of the steles occur in species like *H. clavellata*, in which the axial roots are characterized by an extreme diageotropic habit, and, as has been shown, the degree of diffuseness is measured by the extent of the defection of the root from the vertical position. Hence, a phylogenetic series can be constructed, beginning with the condition noted in early generations of *H. orbiculata* and *H. hyperborea*, and terminating with the condition in *H. clavellata* or *H. dilatata*. Such a series harmonizes the phenomena in axial roots with those in the lateral, rendering it quite certain that polystely is the true explanation in the one as it is in the other.

But there yet remain other facts that are incompatible with any theory of concrescence. A single root-cap clothes the tips of all roots, and behind this root-cap there is a single small-celled meristem, consisting of dermatogen, periblem, and plerome initials. Moreover, the first indication of a root is the appearance of a single meristematic area, and from this alone, without concrescence with any other, the root develops.

The interpretation of the phenomena in polystelic roots in terms of the modern stelar hypotheses, especially of those that attach importance to the differentiated meristematic areas at the growing point is a matter of some interest. The view of Hanstein that the three meristematic areas, dermatogen, periblem and plerome, in the growing point of vascular plants corresponded to the epidermis, cortex, and stele of the mature organ is well known. But it is very evident in these roots that a

primary plerome strand is not wholly young stelar tissue, for on tracing it back in *Habenaria orbiculata*, *hyperborea*, etc., we have found that it passes into secondary plerome strands and extrastelar ground tissue of the same kind, continuous with, and indistinguishable from the cortical tissues. The secondary plerome strands are transformed into steles, each, it may be, with its pith and endodermis, while the ground tissue undergoes no further change. That the plerome is not necessarily the undifferentiated stele has already been proved for certain forms by Schoute (:02), Campbell (:05), and more recently by Conard (:06). But nowhere is this so strikingly the case as in the examples we have described.

In this connection the homologies of the pith and the tissues occupying the axis in polystelic Orchid roots are particularly interesting. There are two theories in regard to the character of pith. One of these regards the pith as always stelar, while, according to the other, the pith in many cases is an extrastelar tissue. The first position has been maintained by Van Tieghem ('86) (except in the case of "gamostely"), Strasburger ('91), Boodle (:01), Tansley and Lulham (:05), and others. Considerable stress has been placed on the correspondence of Hanstein's meristematic areas in the growing point with the areas in the mature portions of the plant. The other view, first proposed by Jeffrey, that the pith is cortical in its homologies in some cases, has for its support the similarity of the cells of the cortex and medulla, their continuity at the gaps, the "dipping in" of the endodermis, certain facts of degeneration, and the incompatibility in certain cases of the Hanstein conception, as noted in the last paragraph. Jeffrey (:00; :02) described the "intrusion" of the cortex into the stele above the point of departure of the leaf traces in seedlings of the Pteropsida, and above the branch traces in the Lycopsida. Faull (:01) described the continuity of the cortex and pith through the ramular gaps in his account of the Osmundaceæ. Chandler (:05) has added further corroborative proof drawn from a study of an extensive series of sporelings.

Further corroboration of the view that the pith may be extrastelar in some cases has been found by the author in his study of the lateral roots of *H. blephariglottis*—a proof amounting to a demonstration. In the majority of Orchid root steles in which a "pith" occurs there is no connection between the pith and the

extrastelar tissues. But in *H. blephariglottis* (Plate I, figure 1) there is an internal endodermis surrounding a pith of quite a different character. On tracing the pith forward from the base towards the root tip (Plate II, figures 2, 3) it has been seen that it is continuous with the extrastelar tissue separating the steles into which the monostele breaks up—a tissue that is unquestionably homologous with the tissue in a similar position in lateral roots of *H. hyperborea, psycodes*, etc. (which are polystelic at their base), and with the tissue separating the two steles in the lateral roots of *H. orbiculata*. The extrastelic character of this tissue is especially evident in the last, for the monostele flattens, bends into a horse-shoe, incompletely enclosing a part of the cortex, and then breaks into two steles of equal size by a constriction or "intrusion" of the cortex from opposite sides (Plate I, figure 6; Plate II, figures 7, 8).

In conclusion, polystely adds another specialized feature to the many possessed by various members of this remarkably specialized family. It is difficult to say how this habit may have arisen, but there is evidently some connection between polystely and the tuberous character of the roots in which it occurs, for it is to be noted that with the increasing size of polystelic roots in succeeding generations there is an increased number of steles in each. The phenomenon, as it exists here, plainly answers to Van Tieghem's definition of polystely. Finally, the conditions existing in these roots must be reckoned with in any stelar hypothesis, for it has been established according to the observations recorded in this paper that the middle and certain more or less radially placed cells belonging to the primary plerome or to the plerome initials directly give rise to extrastelar elements.

SUMMARY

I. There are two types of roots among the terrestrial Orchidaceæ—the monostelic and the polystelic, in Van Tieghem's sense of the terms. In reference to the latter, the term "concrescence" is inapplicable.

II. Polystely has been found in both the lateral and the tuberous roots of *H. orbiculata, H. blephariglottis, H. hyperborea, H. clavellata, H. lacera, H. psycodes, H. virescens, H.*

obtusata, *H. leucophaea*, *H. Hookeriana*; and in the tuberous roots of *H. bracteata* and *Orchis spectabilis*.

III. In the basal portion of the monostele which is ordinarily present in the lateral roots of *H. blephariglottis* a pith and an internal endodermis may occur. The pith in such cases is plainly extrastelar in its homologies.

IV. The plerome initial cells in all polystelic roots are differentiated into stelar and extrastelar tissues.

The above investigation was carried on in the Biological Laboratory of the University of Toronto under the direction of Dr. J. H. Faull, by whom the subject was suggested, and to whom I wish to express my deep obligations for much patient criticism and advice throughout, as also for some of the material. My thanks are due to Professor R. Ramsay Wright for the facilities afforded in the laboratory.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. *H. blephariglottis.* Transverse section through base of lateral root, showing siphonostele with internal endodermis.

Fig. 2. Same stele farther out

Fig. 3. Same stele still nearer the root tip.

Fig. 4. *H. bracteata.* Transverse section of lateral root, showing typical monostele

Fig. 5. *H. clavellata.* Transverse section of stolon, showing ectophloic siphonostele.

Fig. 6. *H. orbiculata.* Transverse section of lateral root, showing monostele beginning to flatten.

PLATE II.

Fig. 7. The same farther out, stele horse-shoe-shaped.

Fig. 8. The same still farther out, after bifurcation.

Fig. 9. *H. hyperborea.* Transverse section through base of lateral root, showing the few large steles.

Fig. 10. *H. hyperborea.* Transverse section of lateral root, showing typical polystelic condition.

Figs. 11, 12, 13. *H. hyperborea.* Transverse serial sections of tip of axial root of plant of an early generation, showing differentiation into secondary pleromic areas.

Fig. 14. *H. blephariglottis.* Transverse section of axial root near tip.

Fig. 15. *H. hyperborea.* Longitudinal section of tip of lateral root.

DIAGRAM 1.

Orchis spectabilis. Diagrammatic representation of vascular system, showing stolon stele supplying young shoot and its axial root; it ends in the meristematic stolon tip which is sheathed by a leaf containing a single stelar trace. There are three root steles: *sh. s.*, stele of adventitious shoot; *s. s.*, stele of stolon; r_1, stele of axial root (r_2, on the opposite side and corresponding to, is not figured); r_3, stele of axial root; *s. l. l.*, stele of sheathing leaf; *s. t.*, tip of stolon; *a. r.*, axial root; *s.*, stolon; *s. l.*, sheathing leaf; *sh.*, adventitious shoot.

DIAGRAMS 2-13.

H. orbiculata. Regional sections of the transition region between shoot and root of a "tuber." A reconstruction would give a figure like Diagram 1, except that the stolon tip is relatively higher up, and there are four root steles instead of three. *Sh. s.*, stele of adventitious shoot; *s. s.*, stele of stolon; r_1 r_2, r_3, r_4, steles of axial root; *s. l. l.*, stele of sheathing leaf; *s. t.*, tip of stolon; *a. r.*, axial root.

DIAGRAM 14.

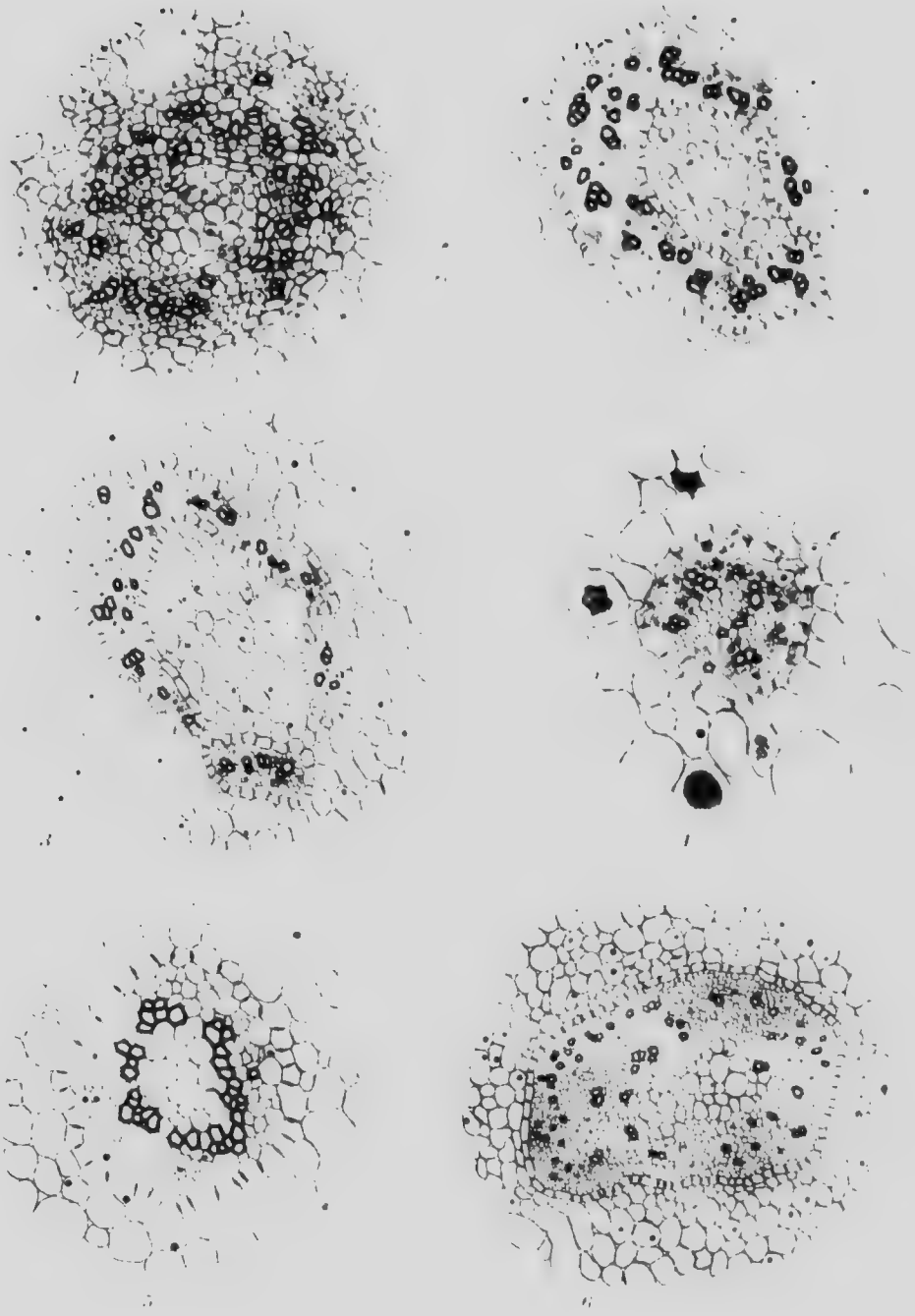
L. clavellata. Diagrammatic representation of vascular system. Note the diffuse origin of the root steles due to the diageotropism of the root. *Sh. s.*, stele of adventitious shoot; *s. s.*, stele of stolon; r_1, r_2, r_3, r_4, r_5, steles of axial root; *s. l. t.*, stele of sheathing leaf; *s. t.*, tip of stolon; *a. r.*, axial root; *s.*, stolon; *s. l.*, sheathing leaf; *sh.*, adventitious shoot.

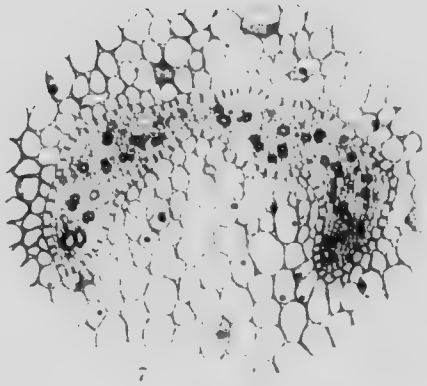
DIAGRAMS 15-26.

H. hyperborea. Regional sections of the transition region between shoot and root of a "tuber." Note that the stolon stele gives off four steles along its length before the region of the root proper is reached. The diagram represents a condition intermediate between Diagrams 2-13 and Diagram 14. *Sh. s.*, stele of adventitious shoot; *s. s.*, stele of stolon; *l. r.*, lateral root; r_1, r_2, r_3, r_4, r_5, r_6, steles of axial root; *s. l. t.*, stele of sheathing leaf; *s. t.*, tip of stolon; *a. r.*, axial root corresponding to shoot.

DIAGRAM 27.

H. hyperborea—plant of an early generation. Diagrammatic representation of vascular system, showing stolon stele supplying young shoot and its axial root; it ends in the meristematic stolon tip which is sheathed by a leaf containing a single stelar trace. Note that the root stele is monostelic at its base, and later divides into two steles. *Sh. s.*, stele of adventitious shoot; *s. s.*, stele of stolon; r_1, r_2 steles of axial root; *s. l. t.*, stele of sheathing leaf; *s. t.*, tip of stolon; *a. r.*, axial root; *s.*, stolon; *s. l.*, sheathing leaf; *sh.*, adventitious shoot; *r.*, monostelic axial root, which lower down bifurcates into r_1 and r_2.





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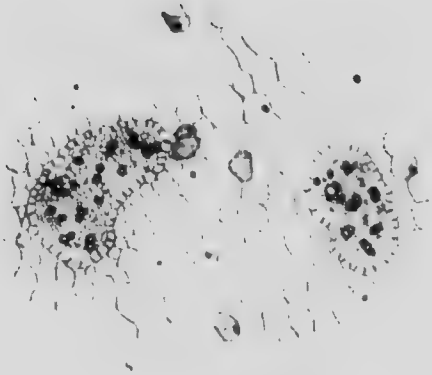

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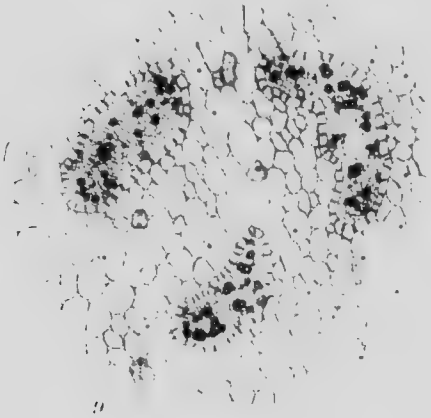

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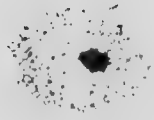

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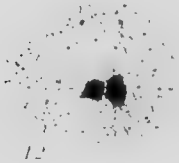

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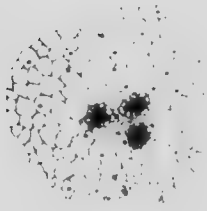

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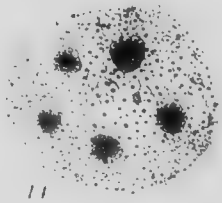

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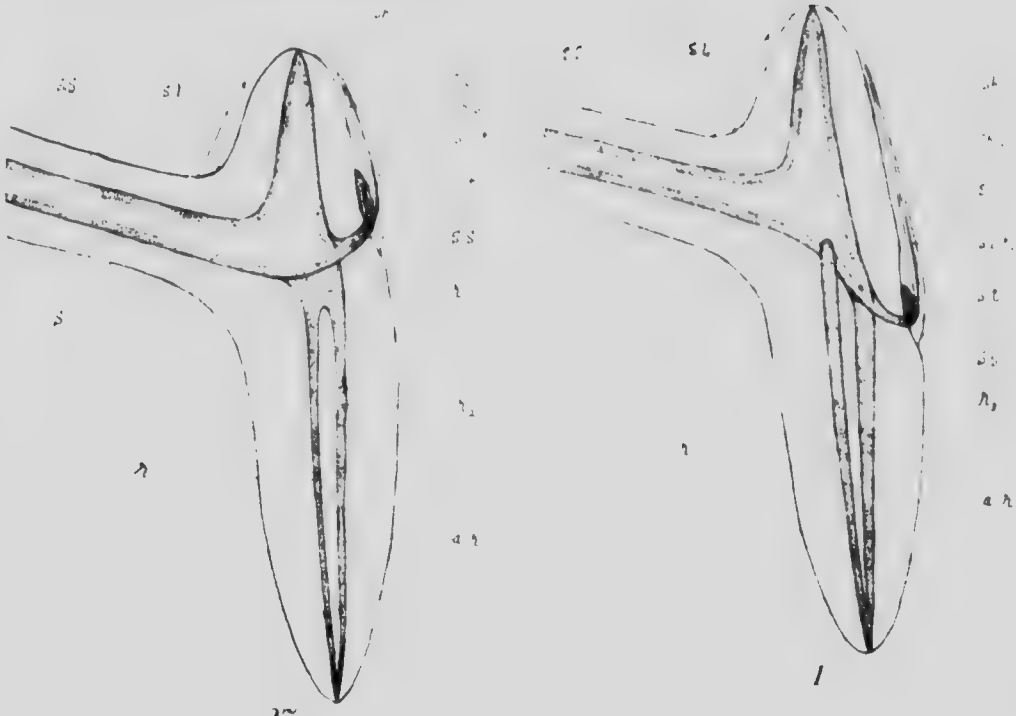

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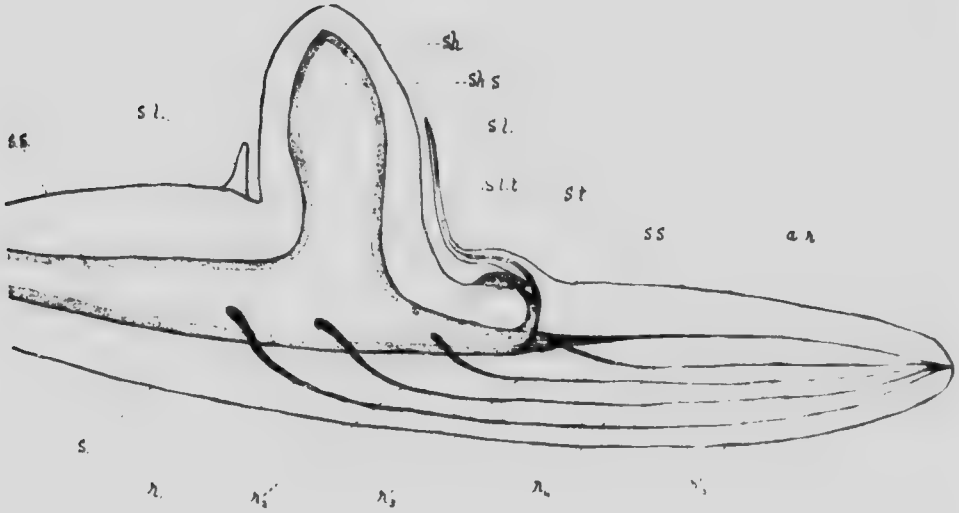

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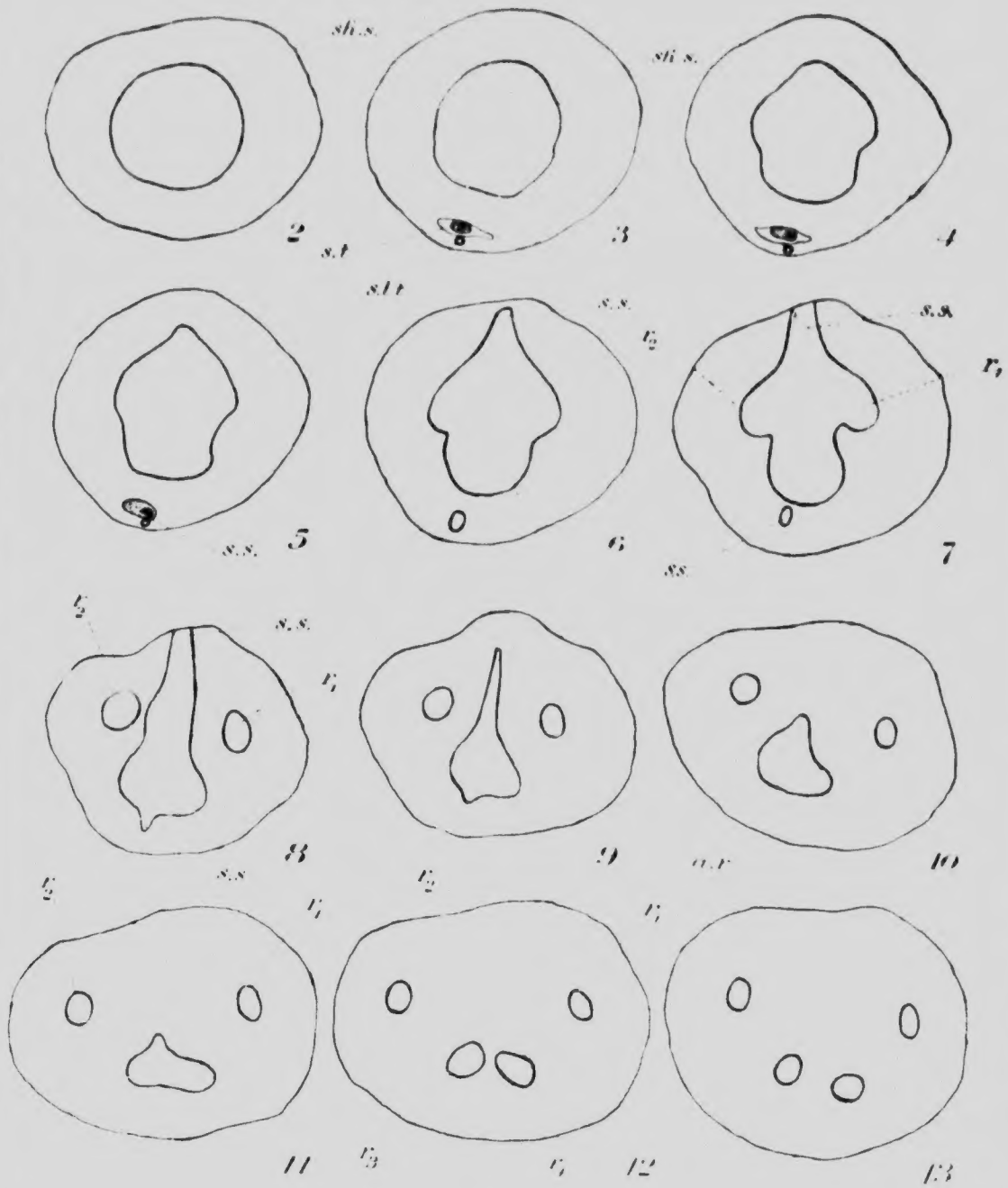
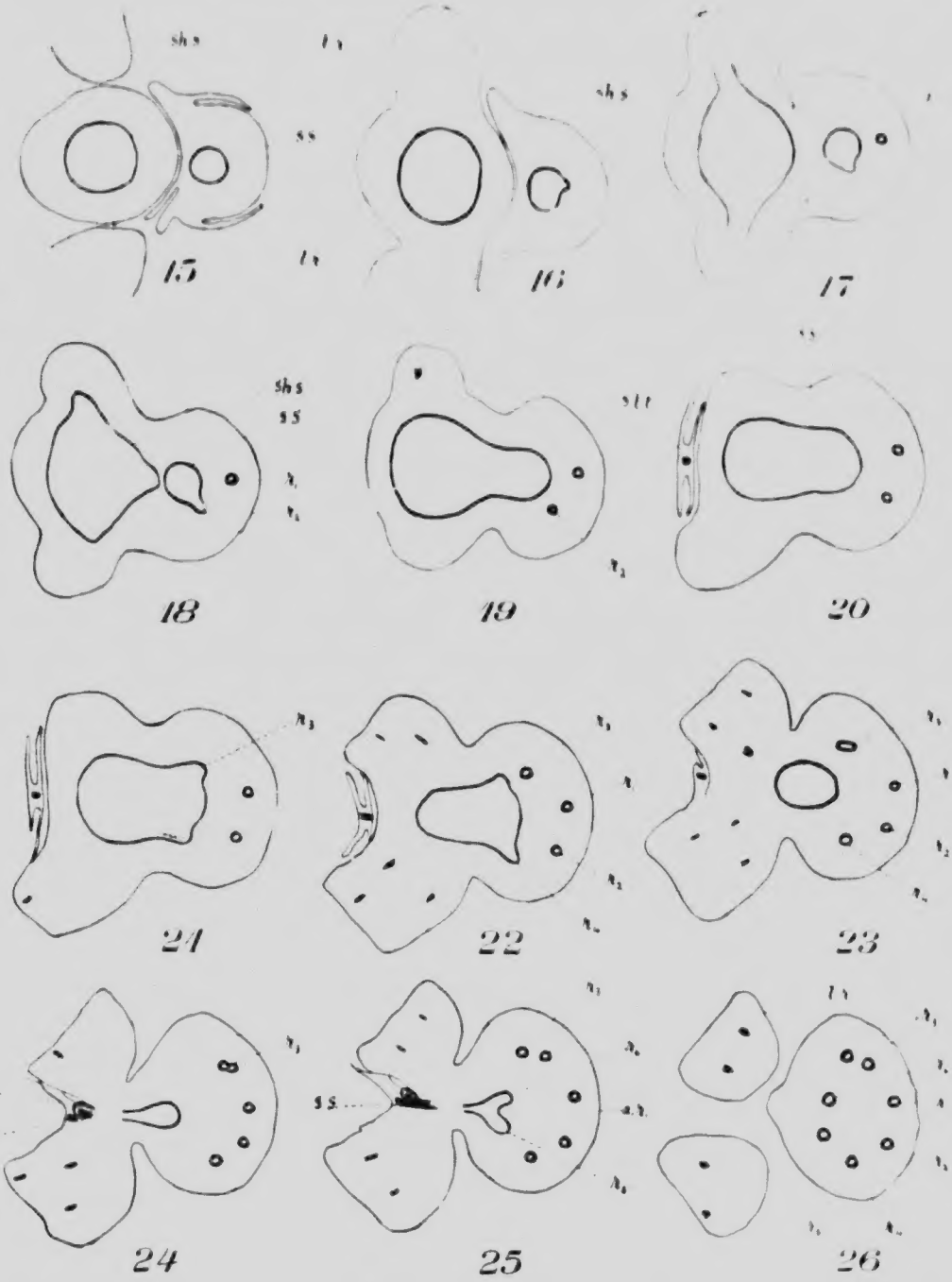
DIAGRAMS 1, 14, 27.



DIAGRAMS 2–13.



DIAGRAMS 15–26.